

ANALYSIS AND COMPARISON OF GAITS IN WHISTLING DUCKS (*DENDROCYGNA*)

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In this paper we analyze the kinetics of the walking gait of four species of whistling or tree duck: *Dendrocygna arcuata*, *D. autumnalis*, *D. bicolor*, and *D. eytoni*. Our aim was to record and compare the gaits of these species and to relate our findings to such features as behavior, habitat usage, and evolution of the species. Closely related species are often useful for studies of adaptive radiation, as evidenced by Lack's (1947) extensive study of insular birds. Whistling ducks provide a wide-ranging group of species for such study, as we have already demonstrated in anatomical-ecological studies of North American *D. autumnalis* and *D. bicolor* (Rylander and Bolen, 1970). The species chosen for the present study are among the better-known dendrocygnids, particularly in terms of habits and ecology. Finally, we include phenograms of the relationships of these species.

METHODS AND MATERIALS

We photographed walking individuals of *Dendrocygna arcuata*, *D. autumnalis*, *D. bicolor*, and *D. eytoni* with a Canon Auto Zoom 618 Super 8 camera at 48 frames per second. The birds were housed in outdoor pens at the Breckenridge Zoo, San Antonio, Texas, and the Wildfowl Trust, Slimbridge, England. Our techniques and analysis generally follow Cracraft's (1971) study of pigeon gaits. We projected film sequences with a Bell and Howell Super 8 Autoload "multi motion" projector and traced the images contained on every other frame (1/24th second).

Our sample of 16 complete strides consisted of three each from three *autumnalis* specimens, three from one *bicolor* specimen, two from a single *eytoni* specimen, and two from a single *arcuata* specimen. These sample strides were selected from a large series of strides because: 1, they were all photographed at suitable distances and angles; 2, they all involved ducks having no obvious locomotor impairments; and 3, they all were executed at about the same velocity. Minimal sampling variation can be achieved when the film sequences for gait analysis are carefully selected. An analysis of variance detected no significant differences ($P > 0.01$) between gaits of the same bird or between gaits of different birds of the same species.

We analyzed the stride through the movements at four joints: the hip joint (femur/acetabulum), the knee joint (femur/tibiotarsus), the intertarsal or ankle joint (tibiotarsus/tarsometatarsus), and the tarsometatarsal/phalangeal joint. Of these, only the movements at the tarsometatarsal/phalangeal joints lacked apparent correlation with specific types of gaits.

The angles at the hip and knee are not directly visible in the photographs. To measure them we located the femur and tibiotarsus by independently locating the acetabulum by the following two methods (Fig. 1). First, we measured the distance between the tip of the tail and the acetabulum in preserved specimens and transferred the equiv-

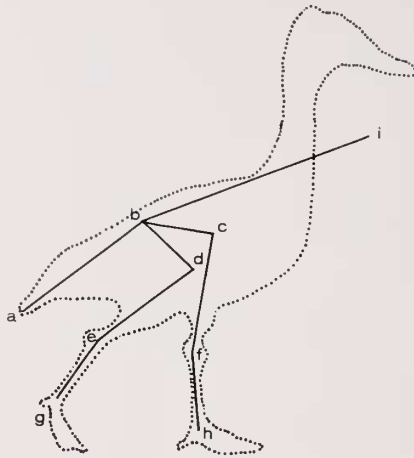


FIG. 1. Whistling duck (*Dendrocygna*) profile indicating two methods for estimating the position of the acetabulum from motion picture tracings. In one method, the distance ab , equivalent to the average tail-acetabular length on preserved specimens, is used to determine the location of the acetabulum. In a second method, if a circle is drawn having its center at d and a radius db , representing the length of the femur, and a corresponding circle having its center at c and a radius cb is drawn on a tracing of the duck at a later point in the stride, then when the two tracings are superimposed, the acetabulum is located at the point where the two circles intersect (i.e. at b). See text for further explanation. This figure also illustrates the angle formed by the anterior ilium and the femur (angle cbi), which necessarily increases when the posture assumes a more vertical bearing in *D. eytoni* and *D. autumnalis*.

alent of this measurement to the tracings. Second, we superimposed two tracings made from frames that showed a duck in two different parts of the same stride. During the time interval between the two frames, the tarsometatarsus changed position (represented by two separate lines (de and cf) on the superimposed tracings). Using the angles at the intertarsal joint (deg and cfh), we drew the tibiotarsus in its two positions; the equivalent length of this bone (calculated from known skeletal proportions and tarsometatarsal length) enabled us to locate its proximal end (the knee joint: c and d). We used the equivalent length of the femur as the radius of two circles centered on the two knee joint positions (bc and bd). The intersection of these circles indicated the location of the acetabulum (b).

In both methods, we necessarily relied on bone measurements from specimens other than those we photographed. Errors attributable to the small variation in bone lengths were calculated at less than two degrees at each of the joints; these do not affect the validity of our results. Likewise, errors attributable to variations in the calculated position of the acetabulum were less than one degree at the joint. Although it is preferable to obtain bone measurements from the subjects actually photographed, we believe our method of analysis is well suited for studying gaits of wild animals on film.

Computations for the phenograms were done using the NT-SYS package of computer programs for numerical taxonomy obtained from F. James Rohlf, State University of

New York at Stoney Brook. The characters used were as follows: 1, plume development; 2, tongue structure; 3, bill spotting; 4, bill coloration; 5, white on wing; 6, patch on wing; 7, foot color; 8, neck striated; 9, markings distinct on downy plumage; 10, downy with bands (not spots); 11, downy plumage base color yellow; 12, tail length; 13, iris color; 14, bill length (relative); 15, wing size; 16, abdominal markings; 17, specialized primaries; 18, tail coverts white-buff; 19, eye ring; 20, spotted breast; 21, voice; 22, occipital tufts; 23, black neck stripe; 24, post-copulatory display; 25, body feathers with spotted tips; 26, throat posture; 27, mutual nibbling; 28, tracheal structure; 29, nocturnal behavior; 30, egg color; 31, egg size; 32, nest in trees; 33, nest over water; 34, perch commonly; 35, nests far from water with regularity; 36, short tarsus to mid-toe ratio; 37, flared pelvis; 38, curved femur; 39, vertical posture; 40, horizontal posture; 41, walking gait; 42, nail shape; 43, lamellae number; 44, bill area; 45, bill epidermis; 46, feeding behavior; 47, upper bill cavity; 48, nares near bill tip; 49, lamellae shape; 50, neck muscles; 51, equilibrium (auditory lobe); 52, equilibrium (semicircular canal); 53, cerebral axis; 54, parallel bill sides; 55, paraglossal size; 56, ceratohyal size; 57, integument lining of maxilla; 58, forehead-bill profile; 59, optic tectum; and 60, semilunar ganglion.

FUNCTIONAL MORPHOLOGY

Although we compared numerous detailed characters of the stride in the four species, only angular displacements at the hip joint (angle *cbi*) reflected an obvious association with differences in gaits (Fig. 2). These differences separate the four species into two well-defined groups: 1, *D. bicolor* and *D. arcuata*; and 2, *D. autumnalis* and *D. eytoni*. The former species initiate

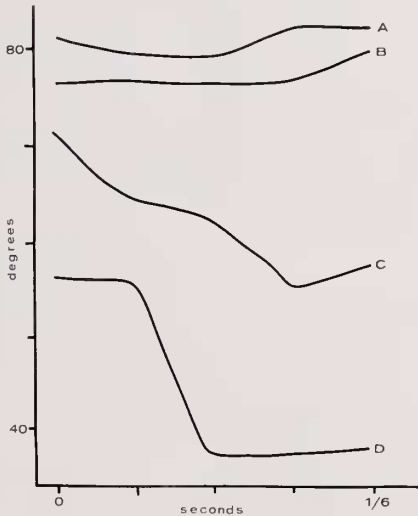


FIG. 2. Sample angular displacements at the hip and knee joints during the first one-fourth of a stride. A, *D. autumnalis*; B, *D. eytoni*; C, *D. bicolor*; D, *D. arcuata*.

TABLE 1

EXTENSION OF KNEE AND ANKLE JOINTS COMBINED (IN DEGREES) AT 1/24 SECOND INTERVALS DURING FIRST HALF OF A STRIDE IN WHISTLING DUCKS (*DENDROCYGNA*).

Time (seconds) ²	Angle <i>bcf</i> + Angle <i>cfh</i> ¹			
	<i>D. autumnalis</i>	<i>D. eytoni</i>	<i>D. bicolor</i>	<i>D. arcuata</i>
0	266	287	211	237
1/24	220	222	211	181
2/24	181	180	129	159
3/24	135	143	118	113
4/24	165	139	144	129
5/24	207	186	185	161
6/24	198	298	237	240
7/24	243	302	237	240
Total degree seconds during first half of stride	59.6	57.0	46.4	48.4

¹ See Fig. 1 for illustration of angles used in this analysis.

² The total number of degree seconds for this half of a stride was derived by graphing the numbers in the table and determining the area under the curves.

³ All four specimens completed the half stride within 1/24 of a second of each other.

their stride with a more horizontally aligned body, as measured by a smaller hip angle (*cbi*), than do the others; moreover, during the first one-fourth of the stride, this angle becomes significantly less than that in the second pair. (We are here defining a "stride" as the movement of one leg from the moment the foot leaves the ground until it next leaves the ground). We found no significant differences between the pairs with regard to hip movements during the remainder of the stride, although we suspect that larger samples of ducks photographed at higher speeds under controlled conditions may reveal less obvious gait characters of importance.

When the sum of angles *bcf* and *cfh* are graphed for the first half of the stride, the areas enclosed by the curves for *autumnalis* and *eytoni* are greater than for *bicolor* and *arcuata* (Table 1). This indicates that *autumnalis* and *eytoni* carry their legs in a more extended condition during this time. The degree of extension of the knee and ankle joints was about the same for all four species during the second half of the stride, when all birds support themselves on a relatively immobile leg as the other leg advances.

The two pairs are also separable on the basis of posture: we consider this closely related to locomotion, although the nature of the relationship is not clear in every respect. *D. autumnalis* and *eytoni* have a relatively vertical posture, whereas *bicolor* and *arcuata* have a more horizontal posture (Fig.

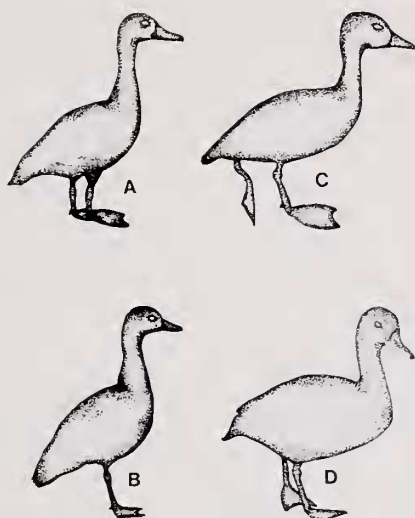


FIG. 3. Profiles of four species of whistling duck showing their characteristic postures on land (see Fig. 2 for legend of species). The profiles were drawn from photographs of living birds.

3). The vertical posture in *autumnalis* and *eytoni* is clearly a function of angle *cbi* (Fig. 1), but it is not necessarily related to the distinctions in angles *bcf* and *cfh*.

In summary, *D. bicolor* and *D. arcuata* initiate their stride and also stand more horizontally than do *D. autumnalis* and *D. eytoni*.

ECOLOGICAL RELATIONSHIPS

The following synopses provide a brief ecological comparison of the four whistling ducks. Of particular relevance to the gait and posture data are each species' walking and swimming habits, their feeding stations, and the location of their nests.

Black-bellied Whistling Duck: *D. autumnalis* is particularly adept at perching and climbing in trees (Rylander and Bolen, 1970), as well as at walking skillfully. Adults swim with their broods, but otherwise swimming is minimal after the breeding season ends: the birds instead wade in shallow water or bask on mud flats. Loafing Black-bellied Whistling Ducks commonly spar among themselves, involving a considerable amount of intense running to or from an opponent. Feeding flights take them to grassy pastures or to grain stubble, sometimes at considerable distances from water (Bolen and Forsyth, 1967). This species, unlike the others discussed, usually

nests in tree cavities at varying distances from water, although we have found some nests on the ground in heavy cover during the course of our field studies. Range: New World.

Plumed Whistling Duck: *D. eytoni* walk long distances gracefully on land but perch in trees only awkwardly and rarely: they seldom dive, except when wounded, and are slow and awkward swimmers (Frith, 1967:80). Lavery (1967) observed that the daily feeding routine starts in the later afternoon, when the birds walk and graze near their roosting sites, then fly to feeding areas elsewhere; they feed mainly on land, eating mostly grasses. This species nests on the ground in the shelter of long grass or a bush, often a mile or more from water. Range: Australia.

Wandering Whistling Duck: *D. arcuata* makes little or no use of tree perches. They are adept swimmers and feed entirely in water, taking small amounts of animal matter and various parts of aquatic plants; their foods are secured by expert and constant diving. Frith (1967:66) once watched several thousand Wandering Whistling Ducks froth the water to a boil as they swam and dove for food. It is primarily in their utilization of foods secured in relatively deep water that the Wandering Whistling Duck remains ecologically separate from the Plumed Whistling Duck throughout their sympatric ranges in Australia (Frith, 1967:83). The nest of this species is a sheltered, grasslined depression on the ground, often far from water. Range: Australia, East Indies (part), and Philippines.

Fulvous Whistling Duck: *D. bicolor* dive readily, and their large feet are structural adaptations presumably related to their swimming habits (Rylander and Bolen, 1970). This species never seems to perch in trees and seldom walks more than a short distance. Fulvous Whistling Ducks feed on the seeds of grasses and sedges common to their aquatic habitats. The species nests in aquatic habitats with dense swards of marsh grasses and other aquatic vegetation. In Louisiana, and elsewhere in North America, they often seek the cover afforded by cultivated rice (*Oryza sativa*) (Lynch, 1943; Meanley and Meanley, 1959). Cottam and Glazener (1959) regularly found nests constructed in grasses rooted in waist-deep water in Southern Texas. Range: New World, Africa, and India.

To summarize, *D. bicolor* and *arcuata* are highly aquatic in their ecology and behavior, and they are characterized by their horizontal posture (Fig. 3) and a more horizontally-initiated gait (Fig. 2, Table 1). In contrast, *D. autumnalis* and *eytoni* are less aquatic and more cursorial in their habits, and they are characterized by their more vertical posture and a less horizontally-initiated gait.

We have thus shown correlations between the functional morphology of

gaits in four closely related species and the behavioral differences that they exhibit. On these bases the four species of Whistling Ducks in this study can be grouped into two pairs, each consisting of one predominately swimming and one cursorial species. One pair, *D. autumnalis* and *bicolor* are sympatric in the New World, whereas the other, *D. eytoni* and *arcuata*, are sympatric in Australia.

PHENETIC RELATIONSHIPS

In order to elucidate possible relationships between the four species on the basis of gait, we prepared a phenogram based first on 60 characters (see Methods). Secondly, we deleted 25 of the 60 and prepared a phenogram based on 35 characters (1 through 35) that we believe have no obvious adaptive significance associated with locomotion or feeding activity. The basis on which to delete characters from the second phenogram was the belief that iris color, for example, could be logically separated from bill shape or foot size as a less than obvious feature of adaptation toward either locomoting or feeding. Hence, such characters as iris color, post-copulatory stance, and downy plumage characters were used in the second phenogram (Fig. 4, lower); such characters as lamellae shape and number, feeding behavior, foot size, and certain features of the skull (see Rylander and Bolen, 1974) were omitted as clearly adaptive.

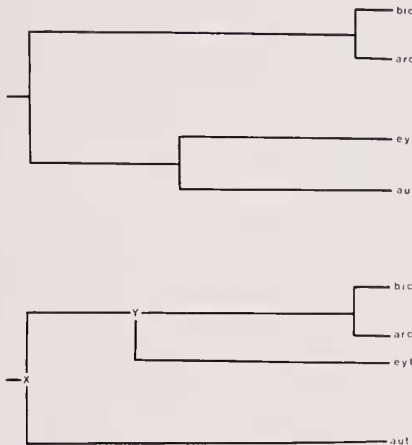


FIG. 4. Phenograms indicating distances between *D. bicolor* (*bic*), *D. arcuata* (*arc*), *D. autumnalis* (*aut*) and *D. eytoni* (*eyt*). The upper phenogram was based on 60 morphological, ecological, and behavioral characters; the lower phenogram was based on 35 of these characters that seemingly have no obvious adaptive significance (see methods section). Points of divergence are indicated by X and Y in the lower diagram.

Basically, the 60 character phenogram indicates that the two aquatic, swimming species (*D. bicolor* and *arcuata*) are more closely interrelated than are the two semiaquatic, cursorial species (*D. autumnalis* and *eytoni*). The 30 character phenogram goes on to show that *D. eytoni* is, in fact, closer to *bicolor* and *arcuata* than to *autumnalis*. The relatively great phenetic distances (Fig. 4) between *eytoni* and *autumnalis*, as well as their widely separated ranges, may be regarded as evidence that the two are not particularly closely related. Thus, their similarity in gait may well be due to parallel evolution, and we suspect that the common ancestor of each species may have had a gait like that of the *D. bicolor-arcuata* group. In other words, we postulate that the cursorial gait is derived, in the case of *D. autumnalis* and *eytoni*; thus, at least in the species of *Dendrocygna* here analyzed, the gait of swimming species may be the more primitive. If we postulate that the gait in *D. autumnalis* and *eytoni* evolved independently, then obviously this and related characters cannot be regarded as having phylogenetic value in studying the relationships of these species.

SUMMARY

The gaits of four broadly distributed species of whistling duck (*Dendrocygna*) were compared. Differences in the angular displacement were greatest at the hip joint and separated the four species into two groups: one group containing the relatively cursorial species, *D. autumnalis* and *eytoni*, and the other the predominately swimming species, *D. bicolor* and *arcuata*. The first group initiates its stride with a larger hip angle and less angular displacement than the second group. The *autumnalis-eytoni* group also assumes a more vertical posture on land than the second group. Consideration of the feeding habits of each species sharpens the ecological distinctions between the two pairs of species.

The possibility that *autumnalis* and *eytoni* evolved the same type of gait independently is suggested by phenetic analyses of the group.

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